

## Phylogenetic relationships of the columbellid taxa *Cotonopsis* and *Cosmioconcha* (Neogastropoda: Buccinoidea: Columbellidae)\*

Helena Fortunato<sup>1</sup>

Smithsonian Tropical Research Institute, Center for Tropical Paleocology and Anthropology, P.O. Box 0843-00153, Balboa, Panama RP, fortunae@si.edu

**Abstract:** Phylogenetic reconstructions are still lacking for many molluscan groups, making evolutionary inferences much weaker. The genera *Cotonopsis* Olsson, 1942 and *Cosmioconcha* Dall, 1913 are part of the so called *Strombina* group, and as such have been used as models to study patterns of speciation and extinction brought about by the rise of the Central American gateway. Earlier work, based on a few species of each genus, pointed towards a very close relationship of these genera, which prompted a complete cladistic analysis, including all species of both genera to evaluate the level of relationship. Cladistic analyses based on shell morphology support the monophyly of the group composed by *Cotonopsis* + *Cosmioconcha*. *Cotonopsis* as currently defined is paraphyletic and includes *Cosmioconcha*. *Cotonopsis* (*Turrina*) keeps its constituency and may retain its subgeneric status. *Cotonopsis* sensu stricto should be redefined to include part of *Cosmioconcha*. *Cosmioconcha* should be subdivided into two groups. One of these groups should be included in *Cotonopsis* sensu stricto. The second group should be given subgeneric status. *Cotonopsis* has a much earlier time of origination and most probably derives from *Cosmioconcha*. Obtained results give support to some of the evolutionary patterns documented earlier for the Neogene molluscan faunas of tropical America and contribute to a better understanding of the Plio-Pleistocene divergence and turnover events related to the rise of the Panamanian land bridge.

**Key words:** gastropods, phylogeny, columbellids, morphology

The family Columbellidae is one of the most diverse and abundant shallow-water gastropod groups. The family has undergone rapid radiation, with over 400 species having evolved since the Danian Paleocene (Keen 1971, Abbott 1974, Radwin 1977, Tracey *et al.* 1993). The *Strombina* group sensu Jung, 1989, is one of the best known columbellid taxa, as it has been used as a model system to study evolutionary trends in species composition, diversity, and ecological patterns related to the Neogene rise of the Panama land bridge (Vermeij 1978, Jackson *et al.* 1993, 1996, Fortunato 1998, 1999). Despite these studies, only recently have the phylogenetic relationships of these taxa been investigated (de-Maintenon 1994, 1999, 2005, Fortunato and Jung 1995, Fortunato 1998). *Cotonopsis* Olsson, 1942, and *Cosmioconcha* (Dall, 1913) are among the genus-level taxa that belong to this group. They are abundant and include mostly recent species with a predominantly tropical American distribution.

In his latest revision, Jung (1989) included *Cotonopsis* but excluded *Cosmioconcha* from the *Strombina* group. Work on the anatomy as well as preliminary cladistic analyses based on a subset of taxa (Fortunato and Jung 1995) confirmed Radwin's (1977) hypothesis of a possible relation-

ship between *Cosmioconcha* and *Strombina* Mörch, 1852 based on radular and shell morphology. These results pointed to a very close relationship between *Cotonopsis* and *Cosmioconcha*. The objective of this paper is to investigate the phylogenetic relationships of these genera, including all fossil and living species, based on shell morphology in order to better understand their history and evolution.

### MATERIALS AND METHODS

This analysis includes all known fossil and Recent species of the genera *Cotonopsis* and *Cosmioconcha* (Table 1). *Cotonopsis* is a very young genus (Jung 1989), with the first known species dating from the early Pliocene of Ecuador. Most of the diversity within *Cotonopsis* developed during the Plio-Pleistocene turnover, around the time of formation of the Panama land barrier. *Cotonopsis* includes 18 species grouped in two subgenera. Only one species is known exclusively as a fossil. Of the 17 living species, 13 inhabit the eastern Pacific basin (Jung 1989), two were reported from the Caribbean region (Houbriek 1983, Petuch 1988, Fortunato 2002b), one was described from the west coast of Africa (Emerson 1993), and a fourth species was found in the Andaman Sea (Kosuge *et al.* 1998, Kronenberg and Dekker 1998, 1999).

\* From the symposium "Relationships of the Neogastropoda" presented at the meeting of the American Malacological Society, held 31 July-4 August 2004 at Sanibel Island, Florida.

<sup>1</sup> Current address: Institut für Geowissenschaften Universität Kiel, Ludwig-Meyn-Strasse 10, D-24118 Kiel, Germany.

**Table 1.** Taxa included in the phylogenetic analyses. Stratigraphic and geographic ranges are given only for ingroup taxa. LM, late Miocene; EP, early Pliocene; LP, late Pliocene. See Table 2 for more information on species of the genus *Cosmioconcha*. Extinct species indicated by an (\*).

Species	Status	Stratigraphic range	Geographic range
<i>Nassarius luteostoma</i> (Broderip & Sowerby, 1829)	Outgroup		
<i>Nassarius antillarum</i> Orbigny, 1842	Outgroup		
<i>Cantliarus ringens</i> (Reeve, 1846)	Outgroup		
<i>Latirus concentricus</i> (Reeve, 1847)	Outgroup		
<i>Cotonopsis (Cotonopsis) panacostaricensis</i> (Olsson, 1942)	Type of species of <i>Cotonopsis</i> Olsson, 1942	LP—Recent	Eastern Pacific (Costa Rica—Colombia)
<i>Cotonopsis (Cotonopsis) edentula</i> (Dall, 1908)		Recent	Eastern Pacific (G. of California—Panama)
<i>Cotonopsis (Cotonopsis) argentea</i> (Houbrick, 1983)		Recent	Caribbean (Dominican Republic)
<i>Cotonopsis (Cotonopsis) crassiparva</i> (Jung, 1989)		Recent	Eastern Pacific (Galapagos Is.)
<i>Cotonopsis (Cotonopsis) deroyae</i> (Emerson & D'Attilio, 1969)		Recent	Eastern Pacific (Galapagos Is.)
<i>Cotonopsis (Cotonopsis) aff. deroyae</i> (Emerson & D'Attilio, 1969)		Recent	Eastern Pacific (Peru)
<i>Cotonopsis (Cotonopsis) esmeraldensis</i> (Olsson, 1964)*		EP	Eastern Pacific (Ecuador)
<i>Cotonopsis (Cotonopsis) jaliscana</i> (Jung, 1989)		Recent	Eastern Pacific (Mexico)
<i>Cotonopsis (Cotonopsis) mendozana</i> (Shasky, 1970)		Recent	Eastern Pacific (Mexico—El Salvador)
<i>Cotonopsis (Cotonopsis) skoglundae</i> (Jung, 1989)		Recent	Eastern Pacific (Gulf of California)
<i>Cotonopsis (Cotonopsis) suteri</i> (Jung, 1989)		Recent	Eastern Pacific (Gulf of California—Mexico)
<i>Cotonopsis (Cotonopsis) aff. suteri</i> (Jung, 1989)		Recent	Eastern Pacific (Mexico—Costa Rica)
<i>Cotonopsis (Cotonopsis) phuketensis</i> (Kosuge, Roussy & Muangman, 1998)		Recent	Andaman Sea (Phuket Is.)
<i>Cotonopsis (Cotonopsis) lindae</i> (Petuch, 1988)		Recent	Caribbean (Barbados)
<i>Cotonopsis (Cotonopsis) monfilsii</i> Emerson, 1993		Recent	Western Africa (Senegal)
<i>Cotonopsis (Turrina) hirundo</i> (Gaskoin, 1852)		Pleistocene—Recent	Eastern Pacific (Gulf of California—Ecuador)
<i>Cotonopsis (Turrina) radwini</i> (Jung, 1989)		Recent	Eastern Pacific (Mexico—Panama)
<i>Cotonopsis (Turrina) turrita</i> (G. B. Sowerby I, 1832)		Recent	Eastern Pacific (El Salvador—Colombia)
<i>Cosmioconcha modesta</i> (Powys, 1835)	Type species of <i>Cosmioconcha</i> Dall, 1913	Recent	Eastern Pacific (El Salvador—Ecuador)
<i>Cosmioconcha palmeri</i> (Dall, 1913)		LM—Recent	Eastern Pacific (Gulf of California—Panama)
<i>Cosmioconcha parvula</i> (Dall, 1913)		Recent	Eastern Pacific (Gulf of California—Panama)
<i>Cosmioconcha rehderi</i> (Hertlein & Strong, 1951)		Recent	Eastern Pacific (Mexico—Ecuador)
<i>Cosmioconcha pergracilis</i> (Dall, 1913)		Recent	Eastern Pacific (Mexico)
<i>Cosmioconcha nitens</i> (C. B. Adams, 1850)		Recent	Caribbean (Cuba, Puerto Rico)
<i>Cosmioconcha calliglypta</i> (Dall & Simpson, 1901)		Recent	Caribbean (Florida, Texas, Puerto Rico)

The earliest known *Cosmioconcha* species dates from the middle Miocene. *Cosmioconcha* was first described as a subgenus of *Amphissa* H. & A. Adams, 1853 (Dall, 1913). Radwin (1978) elevated it to generic rank. *Cosmioconcha* includes seven described species, two inhabiting the Caribbean Sea and five the eastern Pacific region (Table 2, Figs. 1-2). Recent patterns of diversity and abundance of this taxon indicate a radiation similar to other paciphile genera.

Outgroup taxa were selected from Nassariidae, Buccinidae, and Fascioliariidae. Four common taxa from three buccinoidean families were selected as outgroups: Nassariidae—*Nassarius luteostoma* (Broderip & Sowerby, 1829) and *N. antillarum* d'Orbigny, 1842; Buccinidae—*Cantharus ringens* (Reeve, 1846); Fascioliariidae—*Latirus concentricus* (Reeve, 1847). These taxa were selected based on availability and not on the presumption of close phylogenetic relationship.

Forty-two qualitative characters were identified (Appendix 1). Shell sculpture is one of the most characteristic elements of this group, and provides numerous diagnostic characters. Fourteen characters code for type and sculptural details of the teleoconch and body whorl. Presence of shoulder, constriction, inflation, and angulation of the whorls, as well as presence and strength of humps were also coded. Apertural elements (thickness, denticles, apertural and columellar calluses and plicae, parietal ridge) used in traditional taxonomy of this group of gastropods are included here as well. Other characters are general shell shape, type of spire, type and depth of suture, and the relation between the total height and the height of the body whorl. All taxa were coded from direct observation.

MacClade 3.0 (Maddison and Maddison 1992) was used to create the data matrix of 25 taxa and 42 morphological characters (Appendix 2). The heuristic search in PAUP 4.0b10 (Swofford 2001) was used for the analyses, using a random addition sequence with ten replicate searches performed. All characters were unordered and weighted equally. Clade support was assessed through a bootstrap procedure (100 bootstrap replicates with 10 random addition sequences). Tree support was determined using Bremer decay analysis (Bremer 1994) in which progressively longer trees are saved and their consensus calculated in order to see how many more steps are required to collapse branches.

## RESULTS

Cladistic analyses of the data matrix in Appendix 2 yielded six most-parsimonious trees (L=218 steps, CI=0.303, RI=0.513, and RC=0.155). Only the strict consensus tree (Fig. 3) is presented here (the 50% majority rule consensus tree shows exactly the same topology).

The ingroup is monophyletic in all trees, consisting of a single clade grouping all *Cotonopsis* and *Cosmioconcha* species. This clade is defined by fusiform shells with high spire and mostly un-sculptured earlier teleoconch whorls, body whorl mostly un-sculptured, apertures with moderately thickened outer lips, and a well developed, recurved anterior canal.

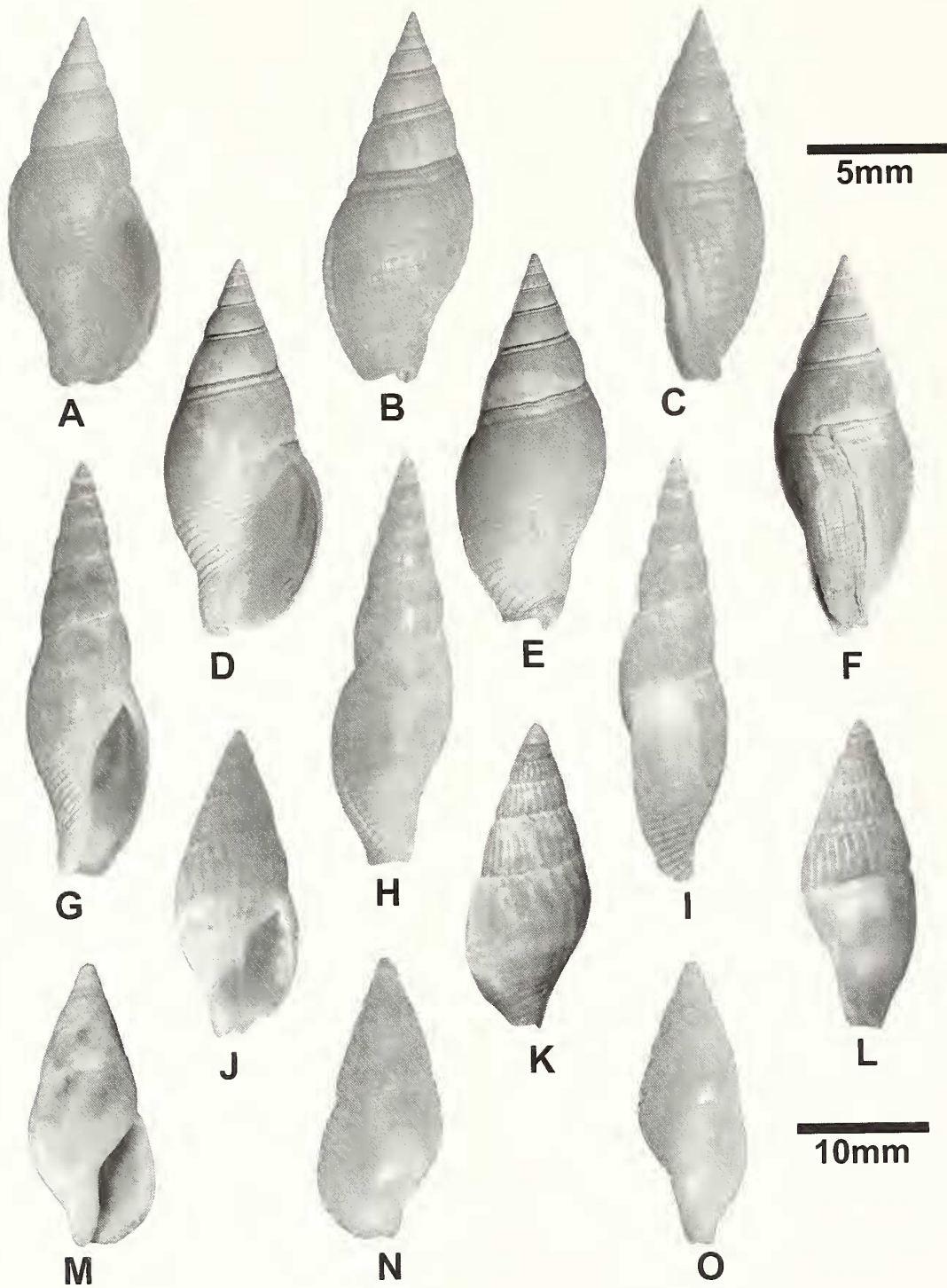
The genus *Cotonopsis*, as traditionally constructed, is paraphyletic and includes the polyphyletic *Cosmioconcha*. The subgenus *Cotonopsis* (*Turrina*) emerges as a monophyletic crown group. *Cosmioconcha* species are grouped in two separate clades within *Cotonopsis*. One clade, which contains the type species of *Cosmioconcha*, emerges in an unresolved trichotomy with a small clade containing the type species of *Cotonopsis* and a large clade that includes *Cotonopsis*, the remaining *Cosmioconcha*, and *Cotonopsis* (*Turrina*).

All species assigned to *Cotonopsis* sensu stricto emerge as a grade that also includes a small clade of three species of *Cosmioconcha*, including its type species. These species have mostly stout shells with axially sculptured late spire whorls and well defined cords at the base of the body whorl. They have broad apertures with denticles and thin outer lip edges.

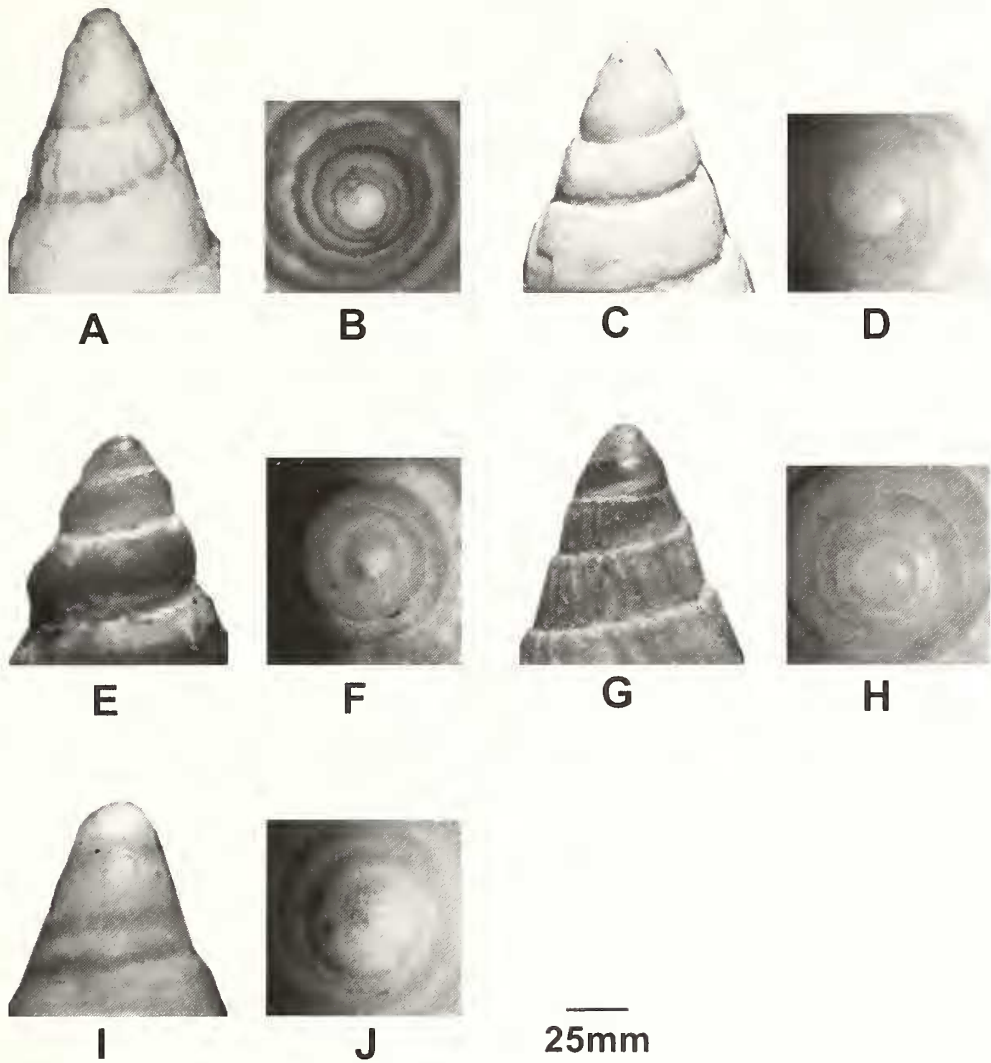
This grade (all *Cotonopsis* sensu stricto + three *Cosmioconcha* taxa) has several smaller groupings. Its base is weakly resolved with several *Cotonopsis* species branching succes-

**Table 2.** Synopsis of species belonging to the genus *Cosmioconcha* Dall, 1913. \*, type species.

Genus	Species	Author & Year	Synonyms
<i>Cosmioconcha</i>	<i>modesta</i> *	Powys, 1835	<i>Buccinum modestum</i> Powys, 1835; <i>Strombina laevistriata</i> Li, 1930
	<i>palmeri</i>	Dall, 1913	
	<i>parvula</i>	Dall, 1913	
	<i>rehderi</i>	Hertlein & Strong, 1951	
	<i>pergracilis</i>	Dall, 1913	
	<i>nitens</i>	C. B. Adams, 1850	<i>Fusus nitens</i> C. B. Adams, 1850; <i>Columbella (Astyris) perpicta</i> Dall & Simpson, 1901; <i>Mitrella perpicta</i> (Dall & Simpson) Woodring, 1928
	<i>calliglypta</i>	Dall & Simpson, 1901	<i>Anaclis calliglypta</i> Dall & Simpson, 1901



**Figure 1.** Species of *Cosmioconcha* Dall, 1913. A-C *Cosmioconcha modesta* (NMB 17442). D-F *Cosmioconcha palmeri* (NMB 17793). G-I *Cosmioconcha parvula* (NMB H18181). J-L *Cosmioconcha rehderi* (NMB H18182). M-O *Cosmioconcha nitens* (NMB 18567). Views are front, rear, and from right side. All specimens belong to the Gibson-Smith Recent collection housed at the Naturhistorisches Museum Basel, Switzerland.



**Figure 2.** Species of *Cosmioconcha* Dall, 1913, protoconchs. A-B *Cosmioconcha modesta*. C-D *Cosmioconcha pahneri*. E-F *Cosmioconcha parvula*. G-H *Cosmioconcha rehderi*. I-J *Cosmioconcha nitens*. Same specimens as in Fig. 1.

sively. Among these are *C. moufilsii* and *C. lindae*, an African and a Caribbean species respectively. The next branch has two small subclades, one with three *Cosmioconcha* and a second one joining two *Cotonopsis* taxa. Next to diverge is the *Cotonopsis* living in the Andaman Sea, followed by another small group formed by two eastern Pacific *Cotonopsis*. The last grouping of this grade joins a Caribbean and two eastern Pacific *Cotonopsis* taxa.

The two other groups are sister clades and are located as crown groups. One of these clades groups, but does not resolve, the three *Cotonopsis* (*Turrina*) taxa. The second group is composed by four *Cosmioconcha* species, among which appear the two Caribbean species. Species of the crown clades have slender shells, almost no axial ornamentation on the spire whorls, and narrower apertures with a

thicker edge. The species of *Cosmioconcha* have more convex spires, numerous denticles on the aperture, and a collar like band below the spire suture. *Cotonopsis* (*Turrina*) taxa are characterized by taller, straight-sided shells and a well developed thickening behind the outer lip. Results of the Bremer decay analysis are plotted onto the strict consensus tree (Fig. 3).

The first round resulted in 284 trees with 219 steps or less. These trees support the monophyly of the entire in-group as well as the monophyly of both crown clades, *i.e.* *Cotonopsis* (*Turrina*) and the four *Cosmioconcha* species. Two small groups that appear among the basal branches (one joining three eastern Pacific *Cosmioconcha*, and another with two *Cotonopsis* *sensu stricto* taxa) are equally supported here. The second round of the decay yielded 6,278 trees, 220

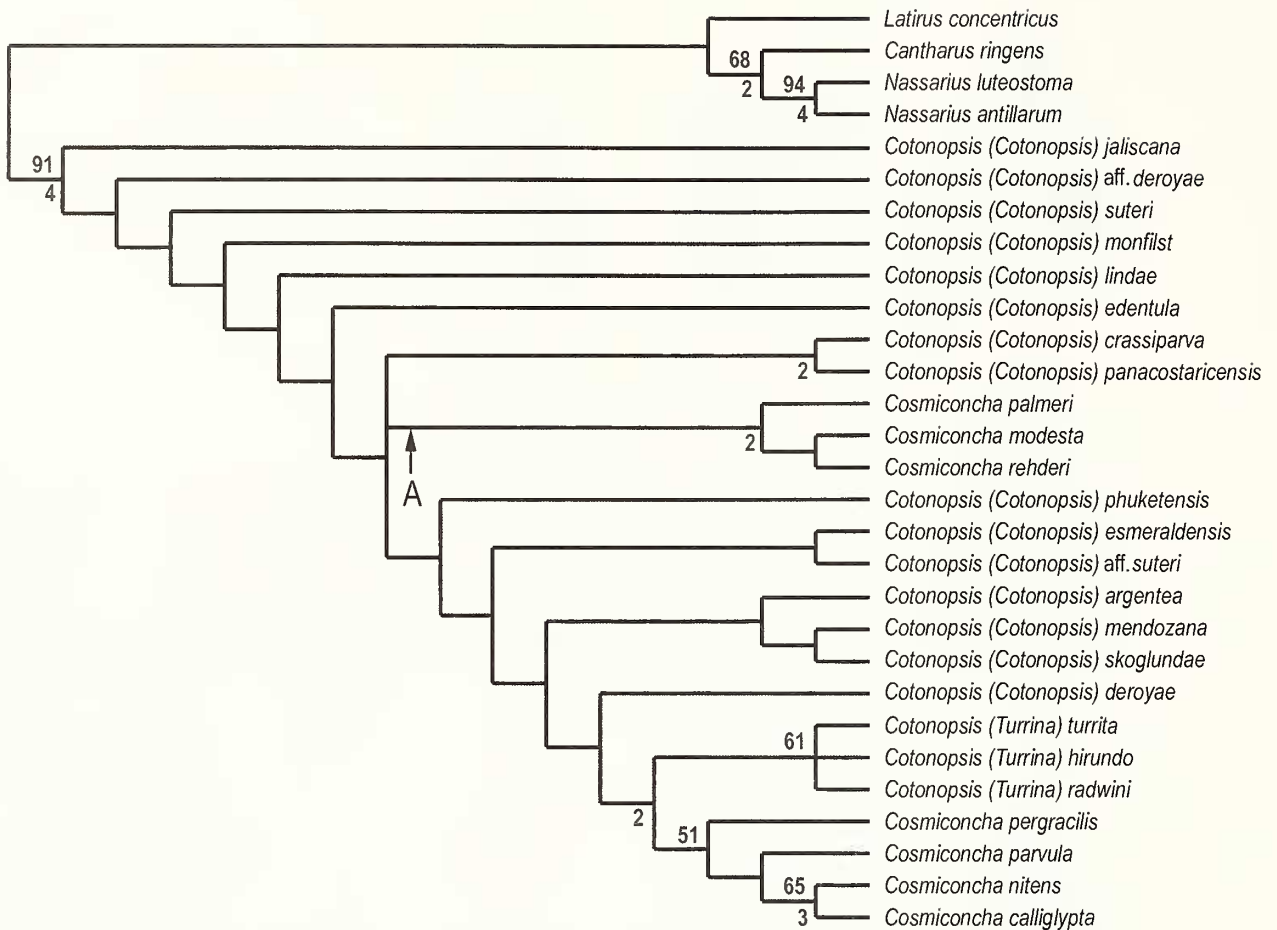


Figure 3. Strict consensus tree of the six most parsimonious cladograms. Numbers below branch nodes are Bremer support values, *i.e.*, the number of extra steps necessary to collapse that node. Nodes without values collapse with one extra step. Numbers above branch nodes are bootstrap support values for that node.

steps or less. The ingroup is still monophyletic but only the group with the two Caribbean *Cosmioconcha* species is supported. The third round yielded 117,655 trees, 221 steps or less. It supports the monophyly of the ingroup but there is no resolution. The fourth round of decay analyses overflowed the memory with over 500,000 trees. The monophyly of the ingroup is still supported here. The bootstrap support for some of the clades is plotted in the strict consensus tree (Fig. 3).

## DISCUSSION

The main objective of this work was to re-evaluate all species that have traditionally been assigned to the genera *Cotonopsis* and *Cosmioconcha*, in order to assess their relationships and the true constituency of these genera. Earlier analyses based on a selected subset of species from each of these genera (Fortunato and Jung 1995) suggested a close relationship of these taxa, confirming Radwin's (1977) hypothesis of a relationship between *Cosmioconcha* and the

*Strombina* group of which *Cotonopsis* is part (Jung 1989). Our objective was to test this relationship, including in the analysis all known species currently included in both genera.

The results of this study indicate that *Cotonopsis* + *Cosmioconcha* form a monophyletic group. *Cotonopsis* as it was initially defined by Jung (1989) is paraphyletic and contains *Cosmioconcha*. Of the two subgenera of *Cotonopsis*, only *Cotonopsis (Turrina)* is monophyletic and retains its entire constituency. *Cotonopsis sensu stricto*, as currently constructed, is paraphyletic. Its status as a monophyletic taxon could be restored only by synonymizing both *Cosmioconcha* and *Turrina*. Alternatively, inclusion of more closely related outgroups might alter the rooting of the tree. Rooting at Position A (Fig. 3) would be required to retain monophyletic *Cotonopsis* and *Cosmioconcha* as sister taxa although the majority of species currently assigned to *Cosmioconcha* would still emerge *Cotonopsis*.

Species assigned to *Cosmioconcha* are divided into two groups. The first group is composed of three eastern Pacific

species, and is located near the base of the tree, among *Cotonopsis* sensu stricto taxa. This group includes the type species, *Cosmioconcha modesta*. The second group is one of the crown subclades and unites two Caribbean and two eastern Pacific species. This group is sister of *Cotonopsis* (*Turrina*).

Within the grade *Cotonopsis* sensu stricto, *C. monfilsii*, a deep water species from West Africa, and *C. lindae*, a shallow water species from Barbados, form adjacent branches but are flanked by eastern Pacific species from California, Mexico, and Peru that have no known fossil record. It is tempting to speculate about the possible existence of geminate pairs [*i.e.*, closely related taxa separated by a barrier (Jordan 1908)] among the extinct fossil ancestors of these taxa. These relationships also suggest an earlier radiation of American species, probably from the eastern Pacific towards the Atlantic before the closure of the Panamanian Strait. Unfortunately, none of these species have a known fossil record which could help calibrate the time of such radiation. However, both the geographic distribution of these species, and the fact that several of the following taxa (within the context of this tree topology) have fossils dating back to the middle Miocene (*i.e.*, *Cosmioconcha palmeri* (Dall, 1913)) suggest that such a radiation may have taken place during the middle Miocene. It is also reasonable to assume the possible existence of fossil lineages yet to be found. Molecular studies could provide an alternative tool to elucidate these relationships.

Three eastern Pacific species of *Cosmioconcha*, including the type species, emerge as a clade. The stem species, *C. palmeri*, has the oldest fossil record of all the species in this study, being known from the middle Miocene deposits of Darien [Radwin, 1977; Panama Paleontological Project (PPP) data]. Based on these results, it is reasonable to assume that *Cotonopsis* sensu stricto is much older than postulated by Jung (1989) in his revision of the *Strombina* group. Jung indicated an early Pliocene age for *Cotonopsis*, based on the occurrence of *Cotonopsis esmeraldensis* (Olsson, 1964) in the early Pliocene of Ecuador. Results of the present analysis indicate that *Cosmioconcha* is part of *Cotonopsis* sensu stricto, thus moving the time of origination of this genus most probably to middle Miocene.

Another closely related small clade unites the Recent *Cotonopsis* (*Cotonopsis*) *crassiparva* and a late Pliocene *Cotonopsis* (*Cotonopsis*) *panacostaricensis* (Olsson, 1942), the type species of *Cotonopsis*.

*Cotonopsis* (*Cotonopsis*) *phuuketensis* (Kosuge *et al.*, 1998), a shallow water species from the Andaman Sea, is the second species in this genus with a distribution outside of tropical America. There are infrequent reports of planktonic larvae crossing the central Pacific barrier (Scheltema, 1978). Most *Cotonopsis* have planktotrophic larvae (exceptions are *C. jaliscana*, *C. esmeraldensis*, and *C. argentea*; authorities in Table 1) able to spend a considerable amount of time in the plankton (Fortunato 2002a). Again, the lack of

fossil data precludes the dating of this dispersal event. Nevertheless, the presence of an early Pliocene species within a sister clade indicates that it may date back to the early Pliocene, at the very least. Here again, molecular data would be useful to help resolve these events.

The next clade comprises *Cotonopsis esmeraldensis* (early Pliocene of Ecuador) and a recent eastern Pacific species, *C. aff. suteri*. This is probably a case of speciation with a switch in developmental mode, as *C. esmeraldensis* is a non-planktotroph whereas its sister species has planktonic larvae. *Cotonopsis esmeraldensis* is the only extinct taxon in the analyzed data set. The basal species of this clade, *C. pukhetensis*, is also a planktotroph. A trans-isthmian event in the history of the group is documented in the next branch of this phylogenetic tree. *Cotonopsis argentea*, a non planktotroph taxon found in deep water of the Dominican Republic coast is the sister taxon of two eastern Pacific species (*C. mendozana* and *C. skoglundae*).

The crown of the tree is composed by two subclades with a relatively strong Bremer and bootstrap support. The stem taxon is *Cotonopsis deroyae*. One of the groups includes the three *Cotonopsis* (*Turrina*) species, confirming the composition and monophyly of this subgenus. The second group, composed by four *Cosmioconcha* species, documents another trans-isthmian event: *C. nitens* and *C. calliglypta* are shallow water taxa inhabiting the Caribbean Sea that diverged from an eastern Pacific taxon.

Based on the obtained results and the phylogenetic reconstruction presented here, *Cotonopsis* sensu stricto, as presently understood, represents a grade that includes several *Cosmioconcha* taxa (*i.e.*, *C. palmeri*, *C. modesta*, and *C. rehderi*), among them the type species of *Cosmioconcha*. All have stout shells with high spires, axially sculptured early teleoconch whorls, body whorls with strong cords on the base, and wide apertures.

The four "*Cosmioconcha*" species that constitute one of the crown groups of the tree are not closely related to the type species of *Cosmioconcha*. These species are characterized by smaller fusiform shells, absence of sculpture on the early teleoconch, absent or weak cords on the body whorl, and narrow apertures. The character "presence of a collar-like band below the suture", traditionally used to unify *Cosmioconcha* taxa is not reliable and should not be given more value than any other morphological character.

*Cotonopsis* is a taxon that reflects the pulse of origination that occurred in the eastern Pacific at the Pleio-Pliocene boundary. Most of the recognized taxa originated during the last two million years, probably along the shallow waters of the eastern Pacific coast. Unfortunately, the stratigraphic record of the eastern Pacific region is not very well preserved (Coates *et al.* 1992, Jackson *et al.* 1993, 1996) and there is no fossil record for most of the known species. *Cosmioconcha* also originated in this region and has a fossil record that

dates back to the middle Miocene. Based on the phylogenetic reconstruction presented here it is reasonable to assume that *Cotonopsis* derives from a *Cosmioconcha*-like ancestor. The group then radiates and speciates with the documented increase in species diversity towards the recent, a pattern well documented for the entire *Strombina* group (Jung 1989, Jackson *et al.* 1993, 1996).

The *Strombina* group has been used as a model system to document patterns of diversification during the Neogene rise of the Panamanian isthmus. Phylogenetic inferences have started to give historical support to earlier studies. The taxa studied here are part of this group and the results confirm the validity of the evolutionary patterns documented earlier (Jackson *et al.* 1993, 1996, Fortunato and Jung 1995, Fortunato 1998, 1999). It is also reasonable to assume the existence of fossil lineages and even Recent taxa yet to be found that could contribute to a better understanding of the natural history of the molluscan fauna of the region and its relationships.

#### ACKNOWLEDGMENTS

This work was presented at the molluscan phylogeny symposium organized by M. G. Harasewych during the AMS meetings, 2004. I thank the institutions that loaned materials for this study. A. Velarde, J. Jara, M. Alvarez, F. Rodriguez, and the Urraca's crew helped with field collections and laboratory work. STRI's digital and SEM laboratory personnel helped with the illustrations. This work was supported by the Scholarly Studies and the Walcott programs of the Smithsonian Institution.

#### LITERATURE CITED

- Abbott, R. T. 1974. *American Seashells*, 2<sup>nd</sup> Edition. Van Nostrand Reinhold Company, New York.
- Bremer, K. 1994. Branch support and tree stability. *Cladistics* **10**: 295-304.
- Coates, A. G., J. B. C. Jackson, L. S. Collins, T. M. Cronin, H. J. Dowsett, L. M. Bybell, P. Jung, and J. A. Obando. 1992. Closure of the Isthmus of Panama: The near-shore record of Costa Rica and western Panama. *Geological Society of America Bulletin* **104**: 814-828.
- deMaintenon, M. J. 1994. Evolution of *Columbella* (Neogastropoda: Columbelloidea) in the Neogene American tropics. *Geological Society of America Abstract with Programs* **26**: A-53.
- deMaintenon, M. J. 1999. Phylogenetic analysis of the Columbelloidea (Mollusca: Neogastropoda) and the evolution of herbivory. *Invertebrate Biology* **118**: 258-288.
- deMaintenon, M. J. 2005. Phylogenetic relationships of the tropical American columbellid taxa *Conella*, *Eurypyrene*, and *Parametaria* (Gastropoda: Neogastropoda). *Journal of Paleontology* **79**: 497-508.
- Emerson, W. K. 1993. A new species of columbellid gastropod from the old world tropics. *The Nautilus* **106**: 147-151.
- Fortunato, H. 1998. Reconciling observed patterns of temporal occurrence with cladistic hypotheses of phylogenetic relationship. *American Malacological Bulletin* **14**: 191-200.
- Fortunato, H. 1999. Biogeography and the tempo of speciation in strombiniid gastropods. Abstracts, 7<sup>th</sup> Congress of the European Society for Evolutionary Biology, II: 107.
- Fortunato, H. 2002a. Reproduction and larval development of the *Strombina* group (Buccinoidea: Columbelloidea) and related gastropods: Testing the use of the larval shell for inference of development in fossil species. *Bollettino Malacologico* **4**: 111-126.
- Fortunato, H. 2002b. The systematic position of *Strombina* (*Cotonopsis*) *lindae* Petuch, 1988 (Gastropoda: Columbelloidea). *The Nautilus* **116**: 59-61.
- Fortunato, H. and P. Jung. 1995. The *Strombina*-group (Neogastropoda: Columbelloidea): A case study of evolution in the neotropics. *Geological Society of America Abstracts with Programs* **27**: A-52.
- Houbrick, R. S. 1983. A new *Strombina* species (Gastropoda: Prosobranchia) from the tropical western Atlantic. *Proceedings of the Biological Society of Washington* **96**: 349-354.
- Jackson, J. B. C., P. Jung, and H. Fortunato. 1996. Paciphilia revisited: Transisthmian evolution of the *Strombina*-group (Gastropoda: Columbelloidea). In: J. B. C. Jackson, A. F. Budd, and A. G. Coates, eds., *Evolution and Environments in Tropical America*. The University of Chicago Press, Chicago. Pp. 234-270.
- Jackson, J. B. C., P. Jung, A. G. Coates, and L. S. Collins. 1993. Diversity and extinction of tropical American mollusks and emergence of the Isthmus of Panama. *Science* **260**: 1624-1626.
- Jordan, D. S. 1908. The law of geminate species. *American Naturalist* **42**: 73-80.
- Jung, P. 1989. Revision of the *Strombina*-group (Gastropoda: Columbelloidea), fossil and living. Distribution, biostratigraphy and systematics. *Mémoires Suisses de Paléontologie* **111**: 1-298.
- Keen, A. M. 1971. *Sea Shells of Tropical West America*, 2<sup>nd</sup> Edition. Stanford University Press, Stanford, California.
- Kosuge, S., P. H. Roussy, and P. P. Muangman. 1998. Report on the fauna of Thailand (1) with the description of a new species (Columbellidae and Buccinidae). *Bulletin of the Institute of Malacology of Tokyo* **3**: 75-76.
- Kronenberg, G. C. and H. Dekker. 1998. A new species of *Cotonopsis* Olsson, 1942, from an unexpected locality (Gastropoda Prosobranchia: Columbelloidea). *Vita Marina* **45**: 11-16.
- Kronenberg, G. C. and H. Dekker. 1999. *Cotonopsis vanwalleghemi* Kronenberg & Dekker, 1998, a junior synonym of *Strombina phuuketensis* Kosuge, Roussy & Muangman, 1998, with some notes on the generic position and colour pattern (Gastropoda Prosobranchia: Columbelloidea). *Vita Marina* **46**: 69-72.
- Maddison, W. P. and D. R. Maddison. 1992. *MacClade: Analysis of phylogeny and character evolution*. Version 3.0. Sinauer Associates, Sunderland, Massachusetts.
- Petuch, E. J. 1988. *Neogene History of Tropical American Mollusks*. The Coastal Education and Research Foundation (CERF), Charlottesville, Virginia.
- Radwin, G. E. 1977. The family Columbelloidea in the western Atlantic. *The Veliger* **19**: 403-417.
- Radwin, G. E. 1978. The family Columbelloidea in the western Atlantic. Part IIb. The Pyreninae (continued). *The Veliger* **20**: 328-344.



Scheltema, R. S. 1978. On the relationships between dispersal of pelagic veliger larvae and the evolution of marine prosobranchs gastropods. *In*: B. Battaglia J.A. Beardmore, eds., *Marine Organisms*. Plenum Publishing Corporation. New York, New York.

Swofford, D. L. 2001. *PAUP: Phylogenetic Analysis Using Parsimony, Version 4.0b10*. Illinois Natural History Survey, Champaign, Illinois.

Tracey, S., J. A. Todd, and D. H. Erwin. 1993. Gastropoda. *In*: M. J. Benton, ed., *The Fossil Record 2*, Chapman and Hall, London.

Vermeij, G. J. 1978. *Biogeography and Adaptation*. Harvard University Press, Cambridge, Massachusetts.

Accepted: 27 March 2007

#### Appendix 1. Character and character state list.

- 1–Shell shape: (0) fusiform (elongate, spire high); (1) strombiform, spire low; (2) buccinoid (stout, spire tapering); (3) columbelloid (stout, spire high)
- 2–Shape of spire whorls: (0) straight sided; (1) straight going to convex; (2) straight going to concave
- 3–Depth of suture: (0) shallow; (1) impressed; (2) incised
- 4–Shoulder on spire whorls: (0) absent; (1) present, inconspicuous; (2) present, strong
- 5–Number of whorls in protoconch: (0) <2; (1) 2-3; (2) >3
- 6–Axial sculpture on early teleoconch whorls: (0) absent; (1) present, inconspicuous and subordinate; (2) present, well developed
- 7–Spiral sculpture on early teleoconch whorls: (0) absent; (1) present, inconspicuous and subordinate; (2) present, well developed
- 8–Axial sculpture on late spire whorls: (0) absent; (1) present, inconspicuous and subordinate; (2) present, well developed
- 9–Spiral sculpture on late spire whorls: (0) absent; (1) present, inconspicuous and subordinate; (2) present, well developed
- 10–Spiral sculpture on body whorl: (0) absent; (1) present, inconspicuous and subordinate; (2) present, well developed
- 11–Axial sculpture on body whorl: (0) absent; (1) present, inconspicuous and subordinate; (2) present, well developed
- 12–Shoulder on body whorl: (0) absent; (1) present
- 13–Cords on base of body whorl: (0) absent; (1) present, weak; (2) present, well developed
- 14–Concavity on central part of body whorl: (0) absent; (1) present
- 15–Constriction on lower part of body whorl: (0) inconspicuously constricted; (1) strongly constricted
- 16–Inflation of body whorl: (0) not inflated; (1) inflated
- 17–Type of sculpture on early vs. late spire whorls: (0) same; (1) different
- 18–Shape of aperture: (0) broad; (1) narrow; (2) slit-like
- 19–Thickness of outer lip: (0) not thickened; (1) slightly thickened; (2) conspicuous thickness
- 20–Teeth on inner surface of outer lip: (0) absent; (1) present, small and inconspicuous; (2) present, strongly developed
- 21–Number of teeth on inner surface of outer lip: (0) none; (1) few (1-5); (2) numerous (>5)
- 22–Posterior canal: (0) absent; (1) present, inconspicuous; (2) present, well developed
- 23–Apertural callus: (0) absent; (1) present, as a slight thickness; (2) present, continuous, well developed
- 24–Columellar denticles: (0) absent; (1) present;
- 25–Parietal callus: (0) absent; (1) present, slightly thickened; (2) present, well developed
- 26–Parietal denticles: (0) absent; (1) present
- 27–Parietal ridge: (0) absent; (1) present, small and inconspicuous; (2) present, well developed
- 28–Sinus on outer lip: (0) absent; (1) present
- 29–Flaring of outer lip: (0) absent; (1) present
- 30–Length of anterior canal: (0) short; (1) intermediate; (2) long
- 31–Width of anterior canal: (0) wide; (1) narrow
- 32–Extension of adapical part of outer lip (aperture edge at suture): (0) outer lip not extended; (1) outer lip somewhat extended after suture
- 33–Shape of anterior canal: (0) slightly curved; (1) strongly curved; (2) straight
- 34–Notch of anterior canal (at the end): (0) shallow; (1) deep depression
- 35–Thickening behind outer lip: (0) absent; (1) present, slight thickness; (2) present, well developed
- 36–Dorsal hump: (0) absent; (1) present, slight thickness; (2) present, well developed
- 37–Edge of outer lip: (0) sharp; (1) rounded
- 38–Hump on left side of outer lip: (0) absent; (1) present, slight thickness; (2) present, well developed
- 39–Repeated thickenings behind outer lip: (0) absent; (1) present
- 40–Plicae on columella: (0) absent; (1) present
- 41–Relation aperture height/total height: (0) aperture < ½ total shell height; (1) aperture much smaller than ½ total shell height; (2) aperture bigger than ½ but smaller than ¾ total shell height
- 42–Collar-like band below spire suture: (0) absent; (1) present

## Appendix 2. Character matrix used for analyses.

Species	Characters					
<i>Nassarinus luteostoma</i>	2111221222	2220120012	2220202010	0022101001	00	00
<i>Nassarinus antillarum</i>	2111222222	2120120002	2220202010	0022101001	00	00
<i>Cantharus ringens</i>	2102021222	2220120001	2211112010	0012200000	00	00
<i>Latirus concentricus</i>	0202021222	2120110001	2010100012	2020000002	10	10
<i>Cotonopsis (Cotonopsis) argentea</i>	0100020200	1010100111	1011101002	0011100000	00	00
<i>Cotonopsis (Cotonopsis) crassiparva</i>	0120120211	0020110022	1120202011	0011100000	00	00
<i>Cotonopsis (Cotonopsis) deroye</i>	0100120011	0010100121	1120102002	1011100000	00	00
<i>Cotonopsis (Cotonopsis) edentula</i>	0120120000	0020111010	0110101012	0111100000	00	00
<i>Cotonopsis (Cotonopsis) jaliscana</i>	0121020000	0110111121	2120102010	0000100000	00	00
<i>Cotonopsis (Cotonopsis) mendozana</i>	0100120000	0010111021	1020201010	0011100000	00	00
<i>Cotonopsis (Cotonopsis) panacostaricensis</i>	0120120211	1020110011	2120102012	0011100000	00	00
<i>Cotonopsis (Cotonopsis) skoglundae</i>	0100?22021	0010001012	2020201002	1011100000	00	00
<i>Cotonopsis (Cotonopsis) suteri</i>	0111210000	0120111021	1120121002	0010100000	00	00
<i>Cotonopsis (Cotonopsis) esmeraldensis</i>	0100020111	0120111122	1020101002	0111101000	10	10
<i>Cotonopsis (Cotonopsis) aff. deroye</i>	0101?10100	1100111011	2110102000	0000101000	10	10
<i>Cotonopsis (Cotonopsis) aff. suteri</i>	0110120111	0120101011	1220001001	0010100000	00	00
<i>Cotonopsis (Cotonopsis) phuketensis</i>	0120110010	0020101111	2020100001	0001100000	00	00
<i>Cotonopsis (Cotonopsis) lindae</i>	0100110100	0020111012	2211102001	0101100000	00	00
<i>Cotonopsis (Cotonopsis) monfilsii</i>	0121212011	0120100022	2111101000	1121101000	00	00
<i>Cotonopsis (Turrina) turrina</i>	0000100010	0010001120	0210102002	0001200100	00	00
<i>Cotonopsis (Turrina) hirundo</i>	0000100010	0010101020	0210001012	1011200000	00	00
<i>Cotonopsis (Turrina) radwini</i>	0000100010	0010111020	1210102010	0011200000	00	00
<i>Cosmioconcha palmeri</i>	0220120010	0120111032	2221200011	0011100000	01	01
<i>Cosmioconcha modesta</i>	3220101011	0010001022	2220201010	0001200000	01	01
<i>Cosmioconcha relideri</i>	3200220210	2020011031	1220201011	0121200000	11	11
<i>Cosmioconcha nitens</i>	0210100010	0010001021	2110100000	0021100000	11	11
<i>Cosmioconcha calliglypta</i>	0200110110	0010011021	2110100000	0021101000	11	11
<i>Cosmioconcha parvula</i>	0200100011	0010101022	2110100002	0001101000	01	01
<i>Cosmioconcha pergracilis</i>	0200200010	0010101021	1110100002	0001101000	01	01